# Seed morphology and colour variation in serotinous Cape Proteaceae

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## Abstract

I investigated seed colour polymorphism in *Leucadendron* is investigated for the possibility of crypsis in a post fire environment. Results were inconclusive, possibly due to a missed opportunity, but do not exclude the possibility of crypsis. Seed predation by birds may be an as yet undescribed and significant phenomenon. Seed morphology and its impact on second phase dispersal is little known, except in a few cases. This was investigated in a comparison of hairy brown *Protea* and black winged *Leucadendron* seeds. This showed that these two types of seed tend to germinate in different habitats. This has implications for interspecific competition and species distribution limits.

## Introduction

Colours of seeds vary widely. Colours such as red and orange and blue are well known for their link to bird dispersal syndrome, showing a strong connection between the colour and dispersal mode. Very little work, however, has been done on the significance of other colours like black, the browns and the yellows, despite them being the most widespread (Grime et al 1981). Even though Grime et al's work concerned only five families, with solely European species, it is still safe to say that very few seeds have conspicuous colours, except in the case of bird dispersal.

Are these inconspicuous colours also linked to dispersal too? In the fire dependent Fynbos of the Western Cape, many of the serotinous species of Proteaceae that release their seeds after fires have dark brown to black seeds (see below). The colours may be directly linked to survival in terms of being cryptic in a post fire environment.

Black seeds could be cryptic on the charcoal-rich post fire substrate, providing protection from predators that search visually, such as seed-eating birds. Predation rates by rodents would probably not be influenced by seed colour because they depend on olfaction and not sight to detect seeds (Hansson 1973; Howard et al 1968) and forage mainly at night. The striped mouse, *Rhabdomys pumilio,* is an exception to this as it is diurnal and thus may depend more on sight than other rodents.

Nystrand and Granström (1997) investigated the effect of seed colour and substrate colour on predation rate. They used the seeds of *Pinus sylvestris*, which range in colour from pale yellow to brown to black. The seed predators in their investigation were two species of ground-feeding finch. The finches recovered more pale than dark seeds on

dark substrates and more dark than pale seeds on pale substrates, showing that seed colour in this species of pine is a cryptic adaptation to the dispersal environment. The authors suggest the variation may be maintained by the fact that, although the main release of *Pinus sylvestris* seeds is after fire, the release of seeds continues for a few years. During this time the substrate changes from charred black to pale as fire debris is eroded.

There is a conspicuous seed colour polymorphism present in the genus *Leucadendron* of the Fynbos Proteaceae. This polymorphism is found among species in this genus that have winged seeds, those of Section *Alatosperma* (Williams 1972). Seed colour in these species is most frequently black, but there are some female plants that produce a lighter colored morph, ranging in colour from pale to dark brown. The seed colour of an individual plant does not vary. The most recent review of *Leucadendron* by Williams (1972) did not record this polymorphism, describing most of the *Alatosperma* as having black seeds.

Seed dispersal in serotinous *Protea* and *Leucadendron* and *Aulax spp* is primarily anemochorous. The propagules take on different varitions on the theme of a seed with extensions of some sort; having either hairs or membranous wings. *Protea* propagules tend to be dark golden-brown and are covered with hairs of variable length. The pollen presenter sometimes remains attached to the seed (Figure 11). *Aulax* propagules are light brown with fine, pure white hairs around the seed (Figure 10). *Leucadendrons* from the *Alatosperma* section, have black, glabrous, winged and sometimes pitted propagules (Figures 2-9). However, propagules from section *Leucadendron* are brown and hairy. All these different types are released when the parent plant dies, usually after

a fire. The initial phase of dispersal can carry the seed up to about thirty meters (Bond 1988), during which the seed extensions act only to slow the rate of descent and thus increase the distance traveled. There is, as yet, no measured difference between the performance of the different wing types at this stage of dispersal. In the second phase seeds are blown along the ground. The hairs act to raise the seed out of the boundary layer of still air at the surface to catch the wind and be transported further. Winged seeds are blown along the ground, but not nearly to the same extent. These are what Bond (1988) refers to as tumbleseeds. He found that second phase dispersal can transport seeds up to 500m from a parent plant, an approximate sixteen fold increase in the dispersal distance.

It is during this second phase of seed dispersal that the different types of seeds might perform differently. If they do then it is hypothesised that different seed types will have different final resting-places. Midgley and von Maltitz (1990) compared seedling distributions of myrmecochorous and anemochorous Proteaceae. They found that anemochores tended to have themselves as nearest neighbours, rather than myrmecochores and *vice versa*, resulting in dispersal into different habitats within the same landscape. These habitats are not defined, they are merely different. There have been no studies comparing germination habitat of different forms of wind dispersed seeds, such as *Proteas* and *Leucadendrons*.

The aims of this investigation were fourfold. The first was to report and describe the nature of the seed colour polymorphism in species of *Leucadendron*, and to look for correlates that might explain it. Associated differences such as seed mass and germination success were also investigated. Secondly, we aimed to determine what

effect substrate and seed colour can have on predation of *Leucadendron* seeds. The third aim was to compare seed colour and morphology variation in serotinous Proteaceae. Linked to this was the fourth aim of determining whether there is any difference in final germination site between different the seed morphologies of *Protea* and *Leucadendron*.

## Materials and Methods

### 1. Seed colour variation in winged species of *Leucadendron*

For clarity, I will refer to the black seed colour morph as "black" and the lighter coloured seed morph as "brown."

To describe the variation of a population of a species we picked cones from at least 57 females, selected along a transect, opened them in drying ovens or with secateurs and recorded the ratio of black to brown seed morphs. We also noted the soil colour of the region in which the population was found. This was performed for 10 species of *Leucadendron* as described in Table 1.

Table 1: Location descriptions of all populations sampled

| **Species** | **Location** | **Soil description** | **Map co-ordinates** | **n** |
|---|---|---|---|---|
| L. crpytocephalum | Viljoen's pass | Orange | 34°05'00"S 19°04'45"E | 108 |
| L. gandogeri | Fern Kloof Nature Reserve | Light | 34°23'50"S 19°15'30"E | 120 |
| L. salicifolium | Hagelkraal farm | Dark | 34°40'00"S 19°40'00"E | 57 |
| L. meridianum | Hagelkraal farm | Light | 34°40'00"S 19°40'00"E | 77 |
| L. coniferum | Hagelkraal farm | Light | 34°40'00"S 19°40'00"E | 69 |
| L. coniferum | Cape of Good Hope Reserve | Light | 34°18'30"S 18°26'10"E | 98 |
| L. laureolum | Cape of Good Hope Reserve | Light | 34°14'10"S 18°24'20"E | 103 |
| L. laureolum | Silvermine | Orange | 34°06'15"S 18°26'10"E | 100 |
| L. xanthoconus | Cape of Good Hope Reserve | Light | 34°18'00"S 18°25'25"E | 117 |
| L. xanthoconus | Silvermine | Light | 34°05'15"S 18°25'30"E | 79 |
| L. xanthoconus | Rotary Way, Hermanus | Light | 34°25'00"S 19°20'00"E | 102 |
| L. uliginosum | George | Orange | 33°54'10"S 22°24'25"E | 72 |
| L. eucalyptifolium | George | Orange | 33°54'10"S 22°24'25"E | 57 |
| L. conicum | George | Dark | 33°54'10"S 22°24'25"E | 67 |

Two *L. coniferum* and *L. laureolum* populations and three *L. xanthoconus* populations were sampled, and one population of each of the other species was sampled.

The seeds were photographed under standard light conditions to demonstrate the

variability in the lighter colour morph. The film used was ASA100 Fuji Superia colour negative.

The mass of the different colour morphs was compared in *L. gandogeri, L. xanthoconus* (Rotary way and Silvermine), *L. laureolum* (Silvermine), *L. meridianum* and *L. coniferum* (both from Hagelkraal). At least 30 seeds were weighed of each morph from each species, except in the case of the brown morph of *L. laureolum*: the cones collected yielded seventeen brown seeds. The masses of the colour morphs were compared with Student's t-tests for independent samples with a 95% confidence limit.

The germination success of black and brown *L. gandogeri* seeds was also compared. Twenty-five seeds of each colour morph were placed in four trays on lightly composted sand, watered heavily and allowed to germinate. The germination success of the two morphs was compared with a $\chi^2$ test performed on a 2x2 [contingency] table, also with a 95% confidence limit.

All statistical tests were conducted with the Statistica software package version 5.1 (1996).

**2. The effect of seed and substrate colour on predation rates**

To test the effect of substrate colour two rows of ten seed patches were placed on the ground in a recently burned area at Silvermine in the Cape Peninsula National Park. The soil at this locality is a light to dark grey sandstone soil. Each patch was 25 by 25 centimeters in size and had ten black *L. laureolum* seeds placed in it. The patches were at least 5 meters apart. The patches in one row were blackened with crushed charcoal

while the others were not blackened. These were left for at least 36 hours on days that were calm, to reduce the possibility of seeds being blown from patches. After this interval the number of seeds remaining in each patch was counted. The missing seeds were assumed to have been eaten.

The effect of seed colour on predation rate was tested in a very similar manner, at the same locality. This time, however, the colour of the seeds was manipulated and the substrate left untouched. Black *L. laureolum* seeds were painted black and white with Reeves non-toxic powder paints. The white paint produced light grey to white seeds when applied. The black painted seeds controlled for any possible effect that the paint might have on the rate of predation. These seeds where placed out in similar rows to those described above, with black seeds in one row of patches and white seeds in the other.

Mann-Whitney U tests were used to compare the mean number of seeds remaining per patch in a row with its counterpart. That is, the row of black seeds was compared with the row of white seeds, and the charcoal substrate row was compared with the natural substrate row.

A laboratory test on the ability of *Rhabdomys pumilio* to detect black *L. laureolum* seeds was also conducted. Two different substrates were placed in the tank: one half pale soil and one half charcoal. Ten seeds were placed on each substrate. One individual was released into the tank in the afternoon and removed the following morning and the uneaten seeds counted. This was done three times with a different rodent each time. The resulting numbers of seeds remaining on each substrate were compared with a Mann-

Whitney U test with a 95% confidence limit.

**3. Seed colour and morphology comparison**

To describe the seed colour and morphology variation among Proteaceae a literature search for seed descriptions was conducted using Rourke (199X), Rebelo (199x) and Williams (1972), resulting in a contingency table of seed colour versus seed morphology. Information on *Protea, Leucadendron* and *Aulax* was included. Colour was classified as either black or not black and seed morphology as either winged or not winged. The goal was to demonstrate that being winged was associated with being black.

**4. Secondary dispersal differences between *Leucadendrons* and *Proteas*.**

Before the fourth aim could be addressed we needed to show that the wind-dispersed seeds of Proteaceae do not germinate in random habitats. This was shown by examining seedling distributions in a burned stand of *L. laureolum* at Silvermine. A straight transect was walked through the stand. When a clump of seedlings was encountered a 25x25cm quadrat was placed over it (position one) and all the seedlings within the area of the quadrat were counted. The quadrat was then placed two meters to the left, (position 2) perpendicular to the line of the transect, and any seedlings in it were counted. This was done 25 times. The resultant lists of seedling numbers for position one and two were compared with a Mann-Whitney U test.

Under the fourth stated aim it was presumed that because of their morphological differences, the seeds of serotinous *Proteas* and *Leucadendrons* would germinate in different habitats. This was tested with seedlings in burned, mixed stands of *Proteas* and

*Leucadendrons* near Hermanus, close to the Rotary way site described in Table 2, and Stanford (34°28'45"S 19°25'50"E) on the south coast of the Western Cape. The two genera are easily distinguished at the seedling stage: *Leucadendrons* have blunt ended cotyledons and hairy first leaves while *Proteas* have more rounded cotyledons, no hairs and a pale red midrib on the early leaves. A straight transect was walked through the stand. When seedlings were encountered they were classified as either *Protea* or *Leucadendron* and the number of seedlings of each genus growing in the surrounding 20x20cm patch was recorded. The patch itself was described as being debris, stump or open. Debris is defined as being a patch of burned debris and charcoal greater than 10x10cm in size and at least 1cm deep. Stump is defined as being within a radius of 15cm from a stump. Open is defined as being greater then 15cm from a stump and having no or very little debris and charcoal. At the Rotary Way burn site there was an additional category of seedling patch, that of leaves. This was defined as a patch of dead leaves, [greater than 20x20cm in size] in which seedlings have been trapped and have germinated. This was done because this site has experienced a less intense burn than the Stanford site, where almost everything barring adult plant skeletons had been burned. Each seedling's nearest neighbour, *Protea*, *Leucadendron* or neither, was also recorded at this site. This provides an additional way of testing if *Proteas* and *Leucadendrons* germinate in different habitats.

For both sites' data $\chi^2$ tests were performed to check for any difference between observed and expected seedling distribution across the germination habitats. The nearest neighbour data was also analysed with a $\chi^2$ test, comparing the observed and expected frequencies of nearest neighbour associations.

## Results

### 1. Seed colour variation in winged species of Leucadendron

The populations that were sampled revealed a high variation in the percentage of brown morphs between species and between populations of the same species. Percentages of females with brown seeds ranged from 0% to 33%. This percentage also varied between populations of *L. laureolum, L. coniferum* and *L. xanthoconus.* (Figure 1)

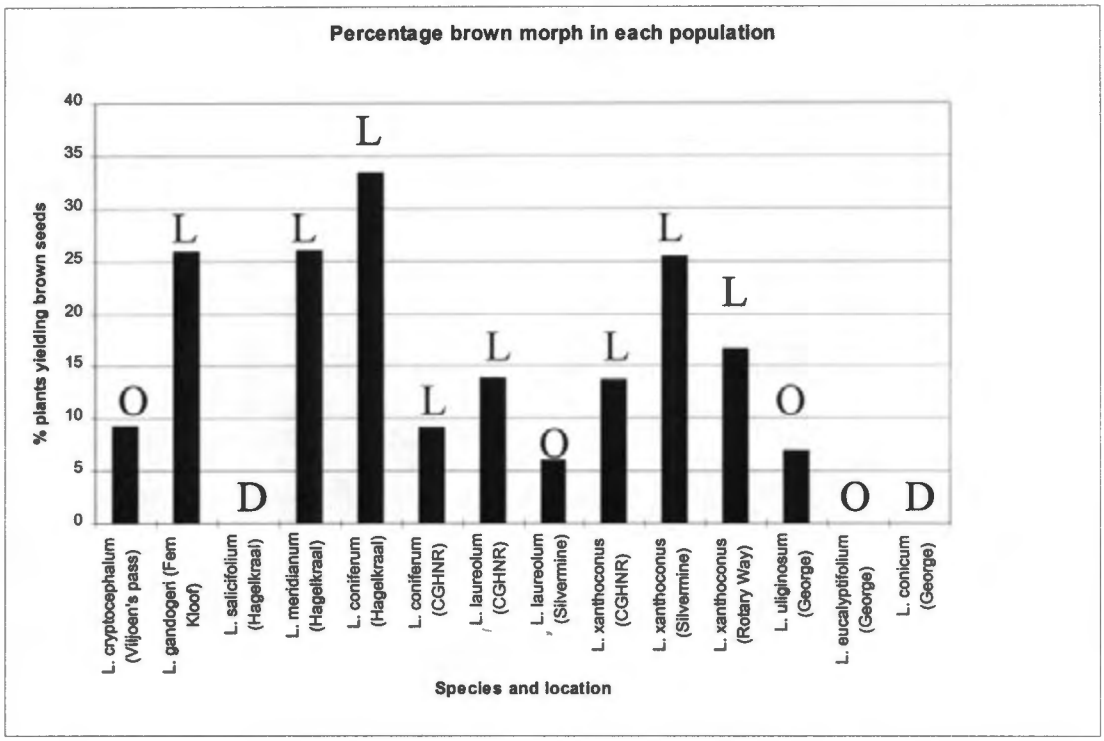


Figure 1: Percentage of female plants with brown seeds in each population, location given in parentheses. Soil colour descriptors given by capital letters: L – light; D – dark; O – orange;

There appears to be a weak correlation between soil colour and ratio of black to brown seeds. Populations of *L. salicifolium, L. laureolum* (when on dark soils), *L. uliginosum, L. eucalyptifolium* and *L. conicum* were all found on dark and orange soils and have the lowest proportions of brown morphs. The remaining populations that are found on lighter soils have the higher proportions of brown morphs.

There is no apparent link between the intensity of the brown colour morph and the soil colour conditions. There is also not sufficient data to test for this statistically as the gradient of soil colour used here is too simplistic, and not enough populations and species were sampled.

Figures 2 to 9, (see end of section) show the nature of the colour variation and also that the brown morph can vary from a light pale brown like that of *L. laureolum* and *L. gandogeri* to the dark brown of *L. crpytocephalum* and *L. uliginosum*. Figures 10 and 11 show the appearance of hairy white *Aulax umbellata* and hairy brown *Protea* seeds respectively.

Seed mass comparisons of the colour morphs in *L. gandogeri, L. laureolum* and *L. xanthoconus* (Silvermine) suggest significant differences in seed mass. The seed masses of *L. coniferum L. meridianum* and *L. xanthoconus* (Rotary Way) were not significantly different (Table2). None of the samples had significantly different variances.

Table 2: Results of seed mass comparisons (N: no significant difference; ** significant difference)

| Species | p (t-test) | | p (F-test for variance) | |
|---|---|---|---|---|
| L. gandogeri | < 0.001 | ** | 0.75 | N |
| L. coniferum | 0.41 | N | 0.59 | N |
| L. meridianum | 0.89 | N | 0.15 | N |
| L. laureolum | < 0.001 | ** | 0.53 | N |
| L. xanthoconus (Rotary way) | 0.67 | N | 0.13 | N |
| L. xanthoconus (Silvermine) | < 0.001 | ** | 0.28 | N |

The $\chi^2$ test comparing the germination success of the two colour morphs of *L. gandogeri* produced a $\chi^2$ statistic of 0.19 (df=1) resulting in p=0.66. At the stipulated 95% confidence limit this indicates that there was no significant difference in germination success between black and brown morphs.

## 2. The effect of seed and substrate colour on predation rates

Manipulation of the substrate colour did not result in a significant difference in remaining numbers of seeds between the black and natural substrates (U=27, p=0.082, 95% confidence limit). Manipulation of seed colour too did not result in a significant difference in remaining seed numbers (U=38, p=0.364, 95% confidence limit)

The test on the ability of *Rhabdomys pumilio* to detect seed revealed that there was no significant difference in the number of seeds eaten off either substrate (U=4 ;p=0.83). This suggests that *R. pumilio* relies on its sense of smell like most other rodents.

### 3. Seed colour and morphology comparison

The data from the literature search were summarised into a 2x2 contingency table (Table 3) The $\chi^2$ test comparing expected and observed frequencies suggested a significant link between being winged and being black ($\chi^2 = 71.85$, df=1, $p<<0.05$).

Table 3: A comparison of seed colour and morphology in species of Proteaceae

| | **Seed morphology** | |
|---|---|---|
| **Seed colour** | Winged | Non-winged |
| Black | 16 spp | 0 spp |
| Non-black | 17 spp | 134 spp |

### 4. Secondary dispersal differences between *Proteas* and *Leucadendrons.*

*Leucadendron* seedlings do not germinate randomly in space in a post fire environment. There are significantly more seedlings germinating in clumps than there are germinating in the open (U=19, $p<<0.05$). This was reconfirmed by the following results of the comparison of germination habitat at the Stanford burn site.

At the Stanford site there was no significant difference in the distribution of *Protea* and *Leucadendron* seedlings between the three described germination habitats ($\chi^2 = 7.4$, df=5, $p<0.193$). There was also a higher proportion of *Protea* and *Leucadendron* seedlings germinating in patches of debris than in the open or next to stumps, reconfirming that germination is not random in space.

At the Rotary Way site there was a highly significant difference in the distribution of *Protea* and *Leucadendron* seedlings between the four described germination habitats ($\chi^2 = 28.69$, df=7, $p<0.000$). Both *Proteas* and *Leucadendrons* tended to congregate near stumps and in debris, but *Proteas* were far more common in the 'leaves' sites. The nearest neighbour analysis showed that there is a significant difference between the expected and observed nearest neighbour associations of *Protea* and *Leucadendron* seedlings ($\chi^2 = 76.06$, df=2, $p<<0.000$). There were far fewer interspecific pairs than expected, suggesting again that *Proteas* and *Leucadendrons* germinate in different habitats as they are found together infrequently.


Figure 2: Seeds of *Leucadendron coniferum*

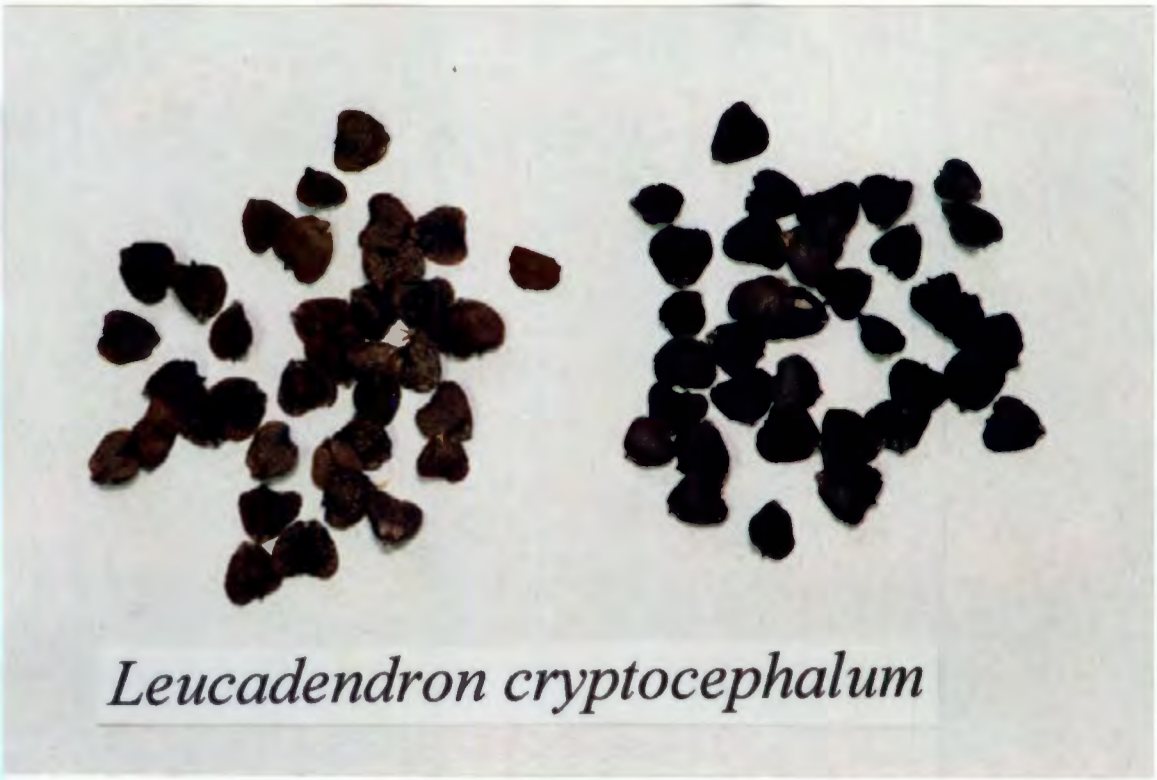


Figure 3: Seeds of *Leucadendron cryptocephalum*


Figure 4: Seeds of *Leucadendron gandogeri*


Figure 5: Seeds of *Leucadendron laureolum*


Figure 6: Seeds of *Leucadendron meridianum*

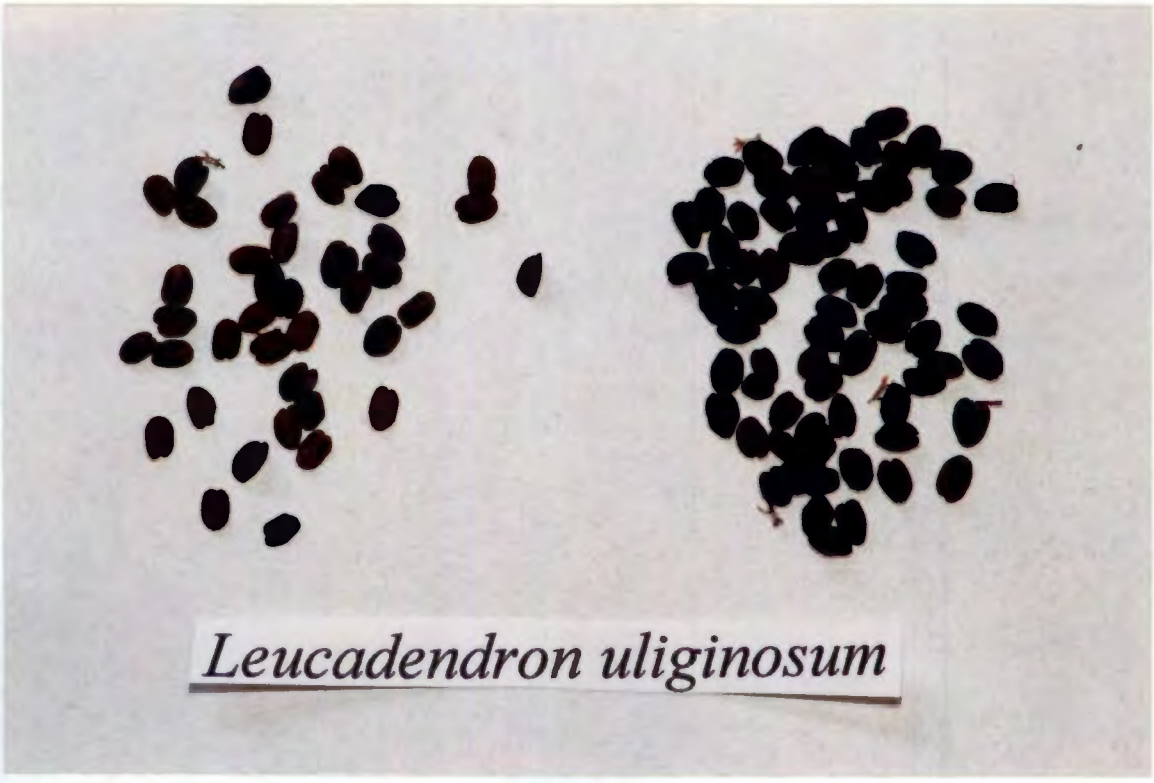


Figure 7: Seeds of *Leucadendron uliginosum*


Figure 8: Seeds of *Leucadendron xanthoconus*


Figure 9: Seeds of *Aulax umbellata*


Figure 10: General Proteaceae seeds

## Discussion

### 1. Leucadendron seed colour polymorphism

The results of the surveys clearly report the presence of a strong seed colour polymorphism in some species of *Leucadendron*. It is maternally inherited as the plants are dioecious and seed coat is derived from the ovary. The amount of polymorphism present in a species and between populations of a species can vary strongly (on Figure 1, compare *L. coniferum* at Hagelkraal and in the Cape of Good Hope Reserve). The intensity of the brown colour morph also varies between species, but is constant within a species. The polymorphism has a possible link to soil colour. Due to lack of data this link is, at present, speculative. More species and more populations of each species would have to be surveyed to confirm the presence of this link.

Soil colour was also not sampled sufficiently. What is needed for confidence in a correlation of colour morphs and substrate colour is an evaluation of the post-fire substrate colour.

Seed mass does not appear to be linked to colour morph, neither does germination success. The colour morphs did not show consistent differences in these respects.

### 2. The effect of seed and substrate colour on predation rate.

Our experiments did not show any significant effect of seed or substrate colour on predation rate, and thus we cannot conclude that the seeds are cryptically coloured. It still remains possible, however, that they are cryptic. We assumed that seeds taken from the patches were eaten, but it is conceivable that there was no predation at all and that missing seeds were merely blown away.

While most of the approaches were logical and had to be tested, we missed the window of opportunity needed to test the crypsis hypotheses properly. This window lies within a week, or less, of a burn when the seeds of *Leucadendrons* are released *en masse*. This is when most of the seed predation is likely to happen. Therefore this is when one can discover exactly what preys on the seeds. The predator is most likely to be a bird as rodent populations are severely reduced by fire (van Hensbergen et al 1992) and birds have the ability to move rapidly into an area after a fire. This, and the confirmation that *Rhabdomys pumilio* relies on scent to detect seeds, suggests that if seed crypsis is present, there is a significant amount of bird predation of seeds in Fynbos. This has not been previously described.

The paint used to manipulate the seeds' colour could also have discouraged seed predators entirely. We did control for the colour, but we assumed that the paint had no discouraging effect. To confirm the presence of crypsis it is therefore necessary to conduct these experiments again, with modification, within the window of opportunity.

**3 and 4. Proteaceae seed colour and morphology: what explains the variation?**

We have shown that winged seeds within Proteaceae are mostly black, and that those seeds without wings, such as nuts and hairy propagules are mostly not black. There is a noteworthy exception to this trend in *Leucadendron platyspermum*. This species is found within *Alatosperma* and has strongly winged seeds, but the seeds are not black, they are a golden brown (Williams 1972). The seeds are not released immediately after fire, but rather after they have germinated in the cone. Seedlings are far less palatable than seeds so predation rate is very low (Williams 1972). The seeds therefore have no

need to be black. This example demonstrates that the consistent blackness of winged *Leucadendron* seeds is likely to be adaptive and not phylogenetic in origin.

We have also shown that *Protea* and *Leucadendron* seeds germinate in different habitats and are clumped within a post fire environment. The distribution of seedlings at the Rotary Way burn site showed this. The Stanford burn site seems to provide contradictory results, but it must be born in mind that the Stanford burn was exceptionally hot and the land was flat. This resulted in a relatively homogenous substrate with few or no patches of leaves and no small bushes. On this substrate any differences in germination site would be very subtle as second phase dispersal of *Proteas* and *Leucadendrons* would be very similar. The burn at the Rotary Way site was cooler and far more debris and small bushes were left. It was also on a slope, with significant run-off. On this sort of substrate differences in second phase dispersal would be more conspicuous.

Why do *Protea* and *Leucadendron* seeds go to different habitats, or, what causes the difference in second phase dispersal? From the data collected one cannot be certain of an answer, but the following hypothetical explanation is presented:

The black, winged seeds do not get blown around easily. One positive outcome of the seed and substrate colour manipulations was confirmation of this. Most of the seeds remained within the patch over the thirty-six hour period and of those that were 'eaten' some were revealed to have been blown out. The blown seeds never traveled further than three meters. However, black winged seeds do travel distances much greater than this from their parent plants. It is therefore hypothesised that they are transported by

surface runoff, along with fine charcoal and fire debris. This supports the belief that crypsis is still a possibility.

The hairy *Protea* propagules, on the other hand have a much greater propensity for being blown around. The surface area of their extensions, the hairs, is relatively greater than that of a winged seed. The hairs also serve to raise the seed higher above the substrate than a wing does. It was with hairy brown seeds that Bond (1988) recorded second phase dispersal distances of up to five hundred meters. He used seeds of *P. repens* that are very similar to those shown in Figure 11. These seeds would blow around until caught by an obstacle such as a stump or pile of sticks and leaves. These seeds would have no need to be cryptically black, as their germination site is infrequently a black charcoal substrate.

This hypothetical explanation is in agreement with the seedling distribution information from the homogenous Stanford site. Here there was no surface run off, only wind powered secondary dispersal, hence the similarity of *Protea* and *Leucadendron* seedling distributions. It also fits the data from the Rotary Way site, where *Leucadendron* seedlings were found more in debris than any other habitat and *Protea* seedlings were found very frequently in piles of leaves and near stumps.

The difference in germination site is relevant to interspecific competition. It offers and explanation why *Proteas* and *Leucadendrons* are able to co-exist in a landscape. Most interspecific competition occurs at the seedling stage, when population numbers are very high and the species are closest together. If this competition is reduced by germination in different habitats then overall interspecific competition is reduced and

co-existence is made possible.

Another effect differential second phase dispersal could have is on distribution across landscapes. There is a weak tendency for winged *Leucadendrons* to be found on pale, nutrient poor soils and *Proteas* to be found on darker, richer soils. Data from Boucher (1978) suggests this. *Leucedendron gandogeri* and *L. xanthoconus* were associated with Champagne, Mispah and Mposa soils (XXX et al, 1991) while *Protea longifolia, P. repens* and *P. lepidocarpodendron* were found on darker, richer Glencoe and Clovelly soils. This could be the result of large-scale selection by visually searching seed predators. The question remains: does seed morphology limit species distributions, and if so, how?

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## References


Bond W.J. 1988 Proteas as 'tumbleseeds': Wind dispersal through the air and over soil *South African Journal of Botany* **54(5)** pp 455-460

Boucher C. 1978 The Hangklip Area II: the vegetation *Bothalia* **12(3)** pp 455-498

Grime J.P., Mason G., Curtis A.V., Rodman J., Band S.R., Mowforth M.A.G., Neal A..M, Shaw S. 1981 A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69** pp 1017-1059

Hansson L. 1973 Fatty substances as attractants for *Microtus agrestis* and other small rodents. *Oikos* **24** pp 417-421

Howard W.E., Marsh R.E., Cole R.E. 1968 Food detection by deer mice using olfactory rather than visual cues. *Animal Behaviour* **17** pp 13-17

Midgley J., von Maltitz G. 1990 Comparisons of seedling distribution patterns of co-occurring wind and ant-dispersed Proteaceae *South African Journal of Ecology* **1(2)** pp 60-62

Nystrand O., Granström A. 1997 Post-dispersal predation on *Pinus sylvestris* seeds by *Fringilla* spp: ground substrate affects selection for seed colour. *Oecologia* **110** pp 353-359

van Hensbergen H.J., Botha S.A., Forsyth G.G., Le Maitre D.C. 1992 Do small mammals govern Vegetation recovery in Fynbos? In: Fire in South African Mountain Fynbos, B.W. van Wilgen, D.M. Richardson, F.J. Kruger, H.J. van Hensbergen (eds.) *Springer-Verlag*

Williams I.J.M., 1972 A review of the genus Leucadendron (Proteaceae) *Contributions from the Bolus Herbarium* **3** The Bolus Herbarium, U.C.T.

Rebelo A.G. 1995 Proteas - a field guide to the Proteas of Southern Africa *Fernwood Press*

Rourke J.P. 1985 The Proteas of Southern Africa *Centaur Publishers*

The Soil Classification Working Group 1991 Soil classification, a taxonomic system for South Africa *Department of Agricultural Development Republic of South Africa*